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THE OVIPOSITION, COCOONING AND HATCHING OF AN ARANEAD, THERIDIUM TEPIDARIORUM C. KOCH.[1]

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During the course of collecting a series of accurately timed stages of the eggs of one of our most familiar spiders, the *Theridium tepidariorum*, I had occasion to accumulate quite a number of observations upon the reproductive habits. Published accounts of such habits in spiders are very few, there is much still unknown, so that it seemed worth while to write up these notes since they are the most extensive yet made upon any single species.

In an earlier contribution[2] I presented an account of this species along with others, and described the moulting, copulation, sperm-induction by the male, cocooning and care of the young. I then described three cases of cocooning, and timed the sequence of cocoons for eight females.

The present observations were made at Woods Hole, Mass., from the fifth to the twenty-sixth of August of the past summer. An unusually large colony of these spiders was found upon an old stone wall in a wood, to which they had probably strayed from some buildings adjacent to one end of the wall. About the first of August the spiders were beginning to form their first cocoons, and upon each of most of the webs of females one or more males were present. Two or three weeks later most of the males had disappeared. My previous study showed that

[1] Contributions from the Zoölogical Laboratory of the University of Texas, No. 76.

[2] "Studies on the Habits of Spiders, particularly those of the Mating Period," *Proc. Acad. Nat. Sci. Philadelphia*, 1903.

there may be frequent copulations before the first act of oviposition, and even between successive acts. But since the males begin to disappear before the full series of cocoons is made, and especially because my captive females produced successive cocoons without the presence of males, and yet these eggs were fertile, it is apparent that copulation before the first act of oviposition suffices for the fertilization of the later sets of eggs. Nearly 150 females were kept in small cages consisting of wooden and paper boxes covered on one side by glass; there was very little mortality among them, and at the end of the month they were manumitted in good condition.

The processes of oviposition and cocooning were observed in part or completely in a large number of cases, and may be summarized as follows. The female commences the cocooning by biting through certain threads in a particular region of the web; she then gathers the cut ends together with her legs, thus making a free space in which to work and at the same time forming a composite thread that serves for the initial suspension of the cocoon as well as of herself during the process of construction. She spins upon the lower end of the suspension thread, and combs out the new line into a fluffy ball; this is the beginning of the base of the cocoon, and the spider employs for the combing mainly the third pair of legs, but to some extent the fourth also. From this point in the operations until the cocoon is nearly completed the spider hangs to lines of the surrounding web by her first and second pairs of legs, with her cephalothorax directed vertically and above the abdomen. When the fluffy fundament of the cocoon base has a diameter somewhat larger than the length of the cephalothorax of the spider, the latter rotates this loose textured ball with her palpi and third pair of legs, and with the fourth pair in alternate application draws a thread out from her spinnerets and applies it to the lower rim of the fluffy ball. She continues this motion until the base of the cocoon has attained the form of an inverted cup, the upper convexity of which is attached to the suspensory line. Towards the close of the base-making her spinning becomes gradually slower. Then she proceeds to oviposit. She lifts herself slightly by contracting the anterior pairs of legs, then

presses her genital aperture against the concavity of the base; a yellow drop of fluid pours out and immediately adheres to the concavity of the base, the eggs rapidly flowing out into it until the whole reaches a size quite equal to that of the spider's abdomen. The spider touches the surface of the egg mass only with the lower surface of her abdomen; during the oviposition there are repeated pressures of the abdomen against the egg mass. The yellow fluid is at first of thin consistency and soon dries upon the eggs; but in drying it does not glue them together. Shortly after the discharge of all the ripe eggs the spider by a few quick contractions detaches her epigynum from the surface of the egg mass, and immediately starts to make the cover of the cocoon, spinning first upon the exposed surface of the egg mass until the latter is covered, then upon the surface of the base also. From her spinnerets she draws out a continuous, compound thread with the fourth legs used alternately, applying this thread to the growing cocoon, while at the same time rotating the cocoon slowly with the third pair of legs (with the occasional help of the second), the spider still hanging to the web above the cocoon by the first pair. Thus the eggs become quickly hidden from sight, by the making of a closely knit cover composed of one continuous thread. Throughout the whole operation the spider keeps pressing the tips of her palpi against the cocoon, which gives her a knowledge of the progress of the progress of the work; there can be no question that she is guided entirely by the sense of touch, for during her labor she is is so placed as to be unable to see the cocoon. Towards the close of the cover making she spins closer, with the result that the exterior surface of the cocoon has the firmest texture. The spinning finished, she feels over the entire surface with her palpi. Rarely does she leave the cocoon hung upon the suspensory thread, usually she carries it higher up into the web and attaches it to the object that roofs the latter.

The finished cocoon varies from yellowish to dark brown in color, and large ones may reach a diameter of 10 mm. It is quite smooth externally, pyriform and usually pointed at the upper end where the suspensory thread was first attached.

More than two hundred cocoons were produced by my spiders,

of which 188 were marked as to the exact or approximate time of oviposition. On a few days I did not commence observations until 6 a. m., and in such cases estimated the time of oviposition of prior cocoons by the state of completion of the cover; but in the majority of cases the precise time of the end of the act of oviposition was determined. From the accumulated data the following results were obtained:

1. *Time of Day of Oviposition.* — This is probably always in the morning and usually in the early morning; in one case a cocoon was made some time between 11 a. m. and 4 p. m., while I was absent from the laboratory, and in this single case oviposition may have occurred later than the noon hour. The next latest case was one at 11.29 a. m. The following table shows the hours of oviposition and the number of cocoons formed in each:

Before 5	5–6	6–7	7–8	8–9	9–10	10–11	11–12
43	51	42	32	33	9	5	2

In the laboratory the spiders experienced about the same light conditions as they did upon the stone wall. Though my lamp was frequently burning at night in the room, and its light wakened the spiders to activity, yet it never induced them to start cocooning. The influence that occasions the cocooning can therefore not be one of amount of light, nor of sudden change from darkness to light. If it were amount of light they should be expected to cocoon at twilight as well as at dawn, yet they never do so. I do not think that cocooning is stimulated by any light condition, but that the stimulus to oviposition may be the oncoming of the warmth of the day after the coolness of the night. My records of cocoons of one and the same individual show that successive cocoons may be formed at different hours of the day, *i. e.*, that one individual does not maintain a particular cocooning hour.

2. *Time Duration of the Act of Oviposition.* — This was timed in 43 cases, the interval being measured from the moment of commencing extrusion of the eggs to the moment of commencing spinning of the cover. In one case it lasted just 2 minutes; in nine cases from 3 to 4 minutes; in twenty cases, from 4 to 5 minutes; in five cases, from 5 to 6 minutes; in six cases from

6 to 7 minutes; in one case, 8½ minutes and in one case, where the spider seemed feeble, 19 minutes. In the majority of cases it lasts from 3½ to 4½ minutes. There is remarkable uniformity in the length of duration of the act, which seems to be quite independent of the number of eggs discharged. After all the eggs have been extruded but while a point of the egg mass surface still adheres to the genital aperture, the spider may continue reiterated ineffectual efforts to discharge further eggs, and how long it continues to do so renders the duration of the process longer or shorter.

3. *Time Duration of the Spinning of the Base.* — This was timed for seventeen cases, showing a variation from 14 to 37 minutes; in eleven of these cases it was between 20 and 30 minutes.

4. *Time Duration of the Spinning of the Cover.* — This was observed in thirty-two cases. In one case the process lasted 27 minutes; in five cases, 40 to 49 minutes; in eleven cases, 50 to 59 minutes; in two cases, 60 to 69 minutes; in three cases, 70 to 79 minutes; in four cases, 80 to 89 minutes; in three cases, 90 to 99 minutes; in one case, 110 minutes; and in one case where the spider lacked the left fourth leg, for 142 minutes. There is, accordingly, considerable variation in the duration of this operation, due not at all to the size of the egg mass, apparently also not to the rate of spinning, but rather to the thickness and firmness of the cocoon which varies greatly. The cover making is usually uninterrupted, but sometimes the spider may pause, then evidently from weariness. It may be that high nourishment would allow the greatest amount of silk secretion, and that in well fed individuals the cocoons be largest and take the most time in the making.

5. *Abnormalities in Cocooning.* — Abnormal cocoons are not rare with wild individuals, and relatively more numerous with my captive specimens. Generally an abnormal cocoon is due to a defect in the spinning of the base; the latter may be too small or too loose, and the spider in working upon it is then liable to pull it out into an irregular form. Again, the issuing egg mass may by accident adhere to a leg of the spider, or even a portion of it become detached from the rest; when this happens the spider

may cease to spin, seemingly being cognizant of something out of the ordinary course. Or the cover may be incompletely made, leaving the egg mass partially exposed, this is apparently due to lack of sufficient space for the spinning operations. Once a mistake is made the spider appears to be unable to rectify it, a fact that I have remarked in my earlier observations (*l. c.*); the whole process appears to be strictly instinctive and the spider seems unable to modify it more than quantitatively, and unable to learn by experience. An individual may make an imperfect cocoon, then construct a following one quite perfect; or the reverse may happen. When the cocoon is particularly irregular, as when the egg mass becomes more or less broken, the spider may either eat the eggs, or may detach them from the web and allow them to fall to the ground.

6. *Time Intervals between Successive Cocoons Formed by the same Individual.* — Of 113 timed intervals between successive cocoons raised in my cages, there was one interval of 2 days, 2 of 3 days, 13 of 4 days, 26 of 5 days, 18 of 6 days, 19 of 7 days, 12 of 8 days, 10 of 9 days, 3 of 10 days, 4 of 11 days, 4 of 12 days, and 1 of 13 days. More than half of the intervals ranged from 5 to 7 days. In all probability the rapidity in the rate of the succession of cocoons depends upon the degree of nourishment of the spider, because some that I purposely starved furnished no cocoons at all. My captives were of course not as well fed as they would have been in the wild state, and though I kept them fairly well supplied with young grasshoppers and locustids this by no means equalled their natural diet in either variety or amount. It is probable that these spiders in a natural state, with normal feeding, would furnish on the average cocoons at intervals of from four to six days. The shortest time in which a succession of 4 cocoons was made by any one of my spiders was 14 days, comprising one interval of 4 days and two of 5 days. The largest number of cocoons I have found in any wild web was eight.

7. *Hatching of the Young.* — Thirty-nine cocoons were kept to determine the time of hatching of the young. Of these, 3 failed to hatch; 3 hatched after an interval of 11 days; 3, of 13 days; 18, of 14 days; 2, of 15 days; 9, of 16 days; and 1, of

17 days. The majority, accordingly, hatched at intervals of from 14 to 16 days. Different generations of cocoons do not have different rates of hatching. Cocoons made on the same day need not hatch at the same time; thus of 8 cocoons made on August 20, 3 hatched in 11 days, 2 in 13 days, 2 in 14 days, 1 in 16 days; and of 11 cocoons made on the morning of August 26, 9 hatched in 14 days, and 2 in 16 days. All these cocoons were removed from the web, placed in separate glass vials, and kept together under the same conditions of light, temperature and moisture. The differences in the rate of hatching are probably due to the difficulties experienced by the young in emerging, for where the cocoon is thinnest the hatching is earliest. Most of the spiderlings emerge in the early morning, but they may come out in the late morning and the afternoon. Each of the few most vigorous spiderlings makes a small circular aperture through the wall of the cocoon, and through these few openings all the rest find their way. The young are at first decidedly positively heliotropic, and it is the light shining into the first made exits that probably guides the less precocious individuals out of the cocoon. The weakest may not emerge until several hours or even days after the most vigorous. In this species, unlike the lycosids, I have found no evidence that the mother aids the young to hatch; for I removed from the webs a number of cocoons immediately after their completion, thus precluding any opening of the cocoon by the mother, yet all of the young made their way out. The mother exhibits some degree of bravery in guarding the cocoon, especially when the latter is newly formed, though never to the extent of allowing herself to be injured, and if she is roughly handled she invariably drops from the web.

8. *Protective Value of the Cocoon.* — I removed eggs, at various intervals after oviposition, from cocoons and placed them in flat glass dishes in the ordinary diffuse light of the laboratory; in all these cases normal spiderlings resulted. Therefore the presence of a cocoon is not necessary to normal development and, further, its value is probably not to exclude the light. One batch of eggs was opened onto a dish of water, where they floated; after a number of days they become covered by a mould that killed

them. Probably the main value of the cocoon is to protect the eggs from enemies, for were the eggs not enclosed they would fall singly or in a mass to the ground, become removed from the guardianship of the mother, and be subjected to a great variety of rapacious foes.

9. *Relation of the Cocoon to the other Forms of Aranead Architecture.* — On this important question I will dwell only briefly at this point, reserving a fuller discussion for later. McCook[1] concludes: "The spinning work of spiders may be classified generally as, first, the Snare, spun for the capture of prey; second, the Enswathment, by which insects are disarmed and prepared for food; third, the Gossamer, used for purposes of aqueous and aerial locomotion; fourth, the Cocoon, spun for the propagation and protection of the species; and fifth, the Nest, which is a domicile more or less elaborate and permanent within and under which the aranead dwells for protection against the exigencies of weather and the assaults of enemies." Menge[2] had previously called attention to the web that the males of certain species spin for the deposition of their sperm, preparatory to charging their palpi with it; this has also been described by me (*l. c.*), and it may be called the "sperm-web." Then Wagner[3] in a most important analysis of the architecture of spiders directed especially towards its phylogenetic significance, has distinguished the web spun by some forms for protection during the moult; and then divides what McCook calls the "Nest" into: "*La retraite*-construction, destinée pour *la demeure de l'araignée*, où elle passe tout son temps et qu'elle ne quitte que pour la chasse. A l'epoque de la ponte cette retraite peut servir de loge au cocon." And into "*Le nid*-construction, destinée au séjour de la femelle et à contenir le cocon." As far as I comprehend this distinction of Wagner's, the "retraite" is a nest made by both sexes, the "nid" one built by the female only. It seems to me questionable whether this distinction of Wagner's is a valid one, and McCook's term "nest" had best be retained without especial subdivision, though surely different kinds of nests may be distinguished.

[1] "American Spiders and their Spinning Work," Vol. 1, Philadelphia, 1889.

[2] "Ueber die Lebensweise der Arachniden," *Neueste Schr. naturf. Ges. Danzig*, 4, 1843.

[3] "L'Industrie des Araneina," *Mém. Acad. Sci. St. Pétersbourg* (VII.), T. 42.

Therefore we have to enumerate: the *cocoon, snare, nest, parachute* (a somewhat more definite term to replace McCook's "gossamer"), *sperm-web, enswathment* and *moult-web.* Of these constructions the cocoon occurs in all species, and probably the nest also; these may then be said to be the most conservative or most persistent kinds of architecture in spiders. It is probable that the nest or protective habitation was the first construction to be elaborated, perhaps first merely some cranny that later became lined with silk by the spider; and that the spider laid its eggs first without lining against the wall of this nest, then later spun upon them a cover of silk. This is of course merely an inference because we know nothing of the ancestors of the modern spiders. But the cocoon, by which is meant the immediate silken envelope of the eggs, may in this way be explained as a derivation of the nest of which it formed at first an integral part; the original base of the cocoon would have been the silken investure of the nest, the cover of the cocoon a later addition. If this suggestion be correct, then the phylogeny of the cocooning would have been as follows: (1) oviposition against the wall of the nest; (2) the addition of a cover to the eggs; (3) a special base spun upon the wall of the nest, the eggs upon which received a cover (a condition realized by certain attids, clubionids and drassids); (4) the formation of a cocoon with base and cover apart from the nest.

Wagner has distinguished two kinds of cocoons: those made of two pieces, and those of a single piece, a distinction based upon the appearance of the completed structure. I would maintain, on the contrary, that it is probable that in all modern araneads the cocoon is spun of two pieces, first a base, then a cover, for I have observed (*l. c.*) this process in lycosids, agalenids, dictynids, theridiids, epeirids and drassids. One may not judge from the form of the finished cocoon as to its mode of construction, and, so far as I know, in all cases where the process has been followed a base is first spun, the eggs oviposited upon it, then a cover made. There seems to be no positive evidence that the cocoon is ever made in a single piece. One of the best diagnostic characters of Araneads is the making by the mother of a silken covering, composed of two pieces, for the protective investment of the eggs.

10. *Parasitic Hymenoptera in the Eggs of Theridium.* — In none of the cocoons raised by my captive spiders were there any parasites, but about one out of every thirty or forty wild cocoons was found to be infected with a tiny hymenopteron, black in color, the males winged and the females wingless, of a length somewhat less than the diameter of an egg of the spider. Prof. Wm. H. Ashmead has kindly identified these as Proctrotrypids, constituting a new species (*montgomeryi*) of the genus *Bœus*. The males hatch some hours or a day in advance of the females, and die soon after the momentary copulation with the latter. The wasps generally hatch out from the cocoons at about the same time the spiders hatch from the uninfected eggs.

Three cocoons, from four to six hours old, were placed in a dish containing wasps that had hatched from other cocoons one or two days previously. The female wasps walked over the surface of the cocoons, continually tapping them with their antennæ; most of the females oviposited into the cover of the cocoons, or at least frequently projected their ovipositors into them. A smaller number made their way into the interior of the cocoons, taking about ten minutes to bore, mainly by rotation of the large and sharp-rimmed head, a small circular aperture into the cocoon. After several of the female wasps had entered in this way I cautiously opened a cocoon and under the compound microscope could observe the wasps piercing the spider eggs with their long, needle-like ovipositors; they seem not to succeed in piercing every egg that they attempt. A single wasp inoculates in this way a considerable number of spider eggs. Only one wasp emerges from any one spider egg, so it is probable that the wasp places only one egg in a spider egg, but I hope to decide this point by a careful study of the infected eggs. Rarely if ever are all the eggs in a cocoon so infected; the infected ones after three or four days turn a dull brown color. If an infected cocoon is kept until hatching in a closed vial, so that neither the emerging spiders nor the hatching wasps can escape, the spiderlings that have escaped infection ultimately catch and eat the adult wasps.